

# Forestry Abstracts

## Nitrogen Cycling in Forested Ecosystems

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### Summary

A description of the compartments, transfers and processes important to the forest cycle. After an introduction, section 2 considers N distribution, uptake and use strategies, followed by a discussion of external inputs, losses and budgets. Later sections describe transfer and cycling processes between ecosystem compartments and within the tree. Finally, the processes of decomposition and mineralization are discussed. Where relevant, the effects of management operations and the possibility of manipulating parts of the cycle for management purposes are considered.

## I. Introduction

Nitrogen (N) is an essential element which is a primary constituent of protein and therefore of the protoplasm of plants and animals. As such its availability is crucially important to the growth of both natural and managed forest, the productivity of which it frequently limits.

Figure 1 shows the principal components of the forest N cycle. The largest reservoir of potentially available N is the atmosphere, but rates of transfer to forest ecosystems are low; relatively little of the N used annually by undisturbed forest comes directly from the atmosphere. However, primary aggrading ecosystems depend on N inputs which are largely atmospheric in origin, while N-deficient ecosystems occur where environmental factors have restricted the input of N by inhibiting plant development and N fixation. Consequently the existing N capital of a forest consists of N accrued during ecosystem development and to a large extent this capital amount determines the pattern and magnitude of N cycling between ecosystem compartments.

Forests may contain large quantities of N, with more than 90% of it organically bound, while plants must obtain most of their N requirement as inorganic forms which comprise less than 1% of the total. This marked contrast between a large N capital and small amounts of available N typifies forest ecosystems. Continued forest growth depends upon the maintenance of this available N pool and its efficient use, which are achieved by the input and mineralization of plant litter and N cycling within the forest biomass.

## II. Nitrogen distribution, uptake and use efficiency

### 1. Nitrogen distribution

An accounting approach which compartmentalizes ecosystem N can be useful since it identifies the principal N pools. Pool size may not be related to rate of turnover or functional importance in the cycling process.

Ecosystem productivity and nutrient accumulation have been the subject of numerous research papers and much of this material has been presented in review articles: for evergreen conifers and deciduous broadleaves, Rodin & Bazilevich (1967), Larcher (1975), Keeney (1980), Cole (1981), Cole & Rapp (1981), and Heal *et al.* (1982); for evergreen conifers, Fogel (1980) and Gosz (1981); for deciduous broadleaves, Melillo (1981).

Table 1 gives some general values for evergreen conifers and deciduous broadleaves. Despite the considerable range certain similarities are apparent. Most N is in the soil, around 80%, while N in the tree biomass and in the forest floor are each approximately 10%. The root system is clearly important; it accounts for 15-30% of tree biomass (Fogel, 1983; Persson, 1983) or 19-32% of tree N (Henderson & Harris, 1975; Wells & Jorgensen, 1975; Fogel, 1980). Additionally, mycorrhizas can make up 8% of the tree biomass, with mycorrhizal roots accounting for 25% of tree N and non-mycorrhizal roots 7% (Fogel, 1980).

Considering ecosystem compartments solely in terms of standing-crop values can lead to underestimates of the importance of small but rapidly turned-over compartments. This problem is avoided if compartments are also considered in terms of productivity, which takes account of rates of turnover. In particular, the importance of the fine root system is underestimated if only the standing crop is considered. Fogel & Hunt (1983) found that 75% of tree uptake in a young Douglas fir stand went into root and mycorrhizal turnover, although the standing-crop values represented only 35% of tree N.

### 2. Forms of uptake

N uptake is dealt with extensively by Nye & Tinker (1977), Clarkson & Hanson (1980), Kirkby (1981), Novoa & Loomis (1981), and Mengel & Kirkby (1982). Forms of N, both inorganic and organic, are discussed by Nommik & Vahtras (1982), Stevenson (1982), and Young & Aldag (1982).

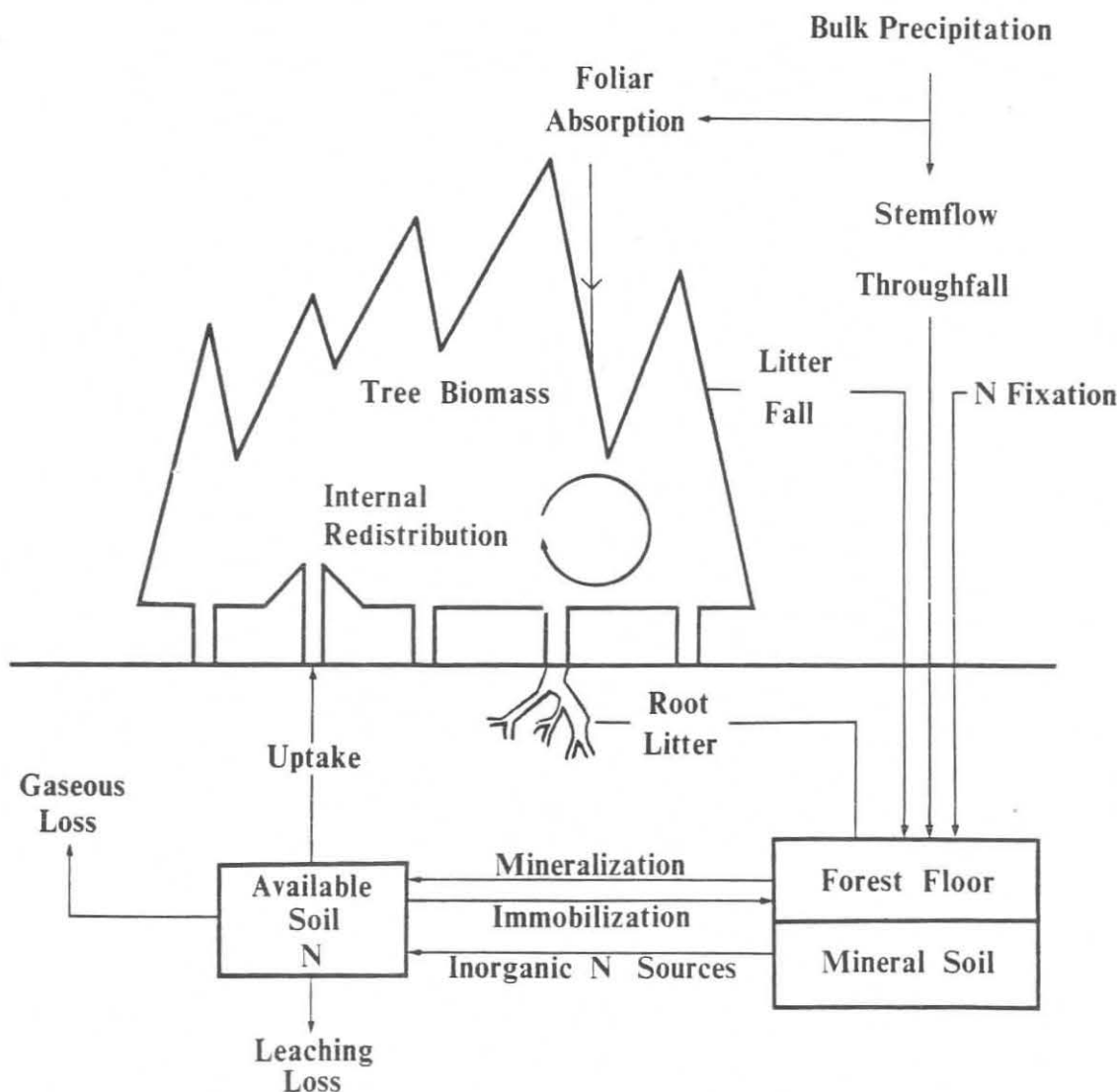


Fig. 1 The forest nitrogen cycle

Under the conditions which prevail in many forest soils (low pH and intense microbial competition for inorganic N), the conversion of ammonium to nitrate by nitrifying organisms is low. Consequently ammonium is the dominant form of inorganic N available to plants. Ammonium is a cation, held by the soil cation exchange complex; such exchangeable ammonium is freely available to plants. It is normally present in the range 0-5 p.p.m. (Bowen & Smith, 1981), with only a little occurring as the ionic form in the soil solution, <2 p.p.m. (Cole, 1981). Solution concentrations are usually 0-0.001 M (Nye & Tinker, 1977). Together these available forms represent less than 2% of total soil N (Russell, 1973; Brady, 1974; Pritchett, 1979; Jenny, 1980). Some soils may also contain appreciable amounts of fixed or non-exchangeable ammonium, up to 25% of total surface soil N (Kudeyarov, 1981). While 30-60% of this fixed N may be potentially available to plants, its importance in forest ecosystems is poorly documented (Kudeyarov, 1981; Nommik, 1981; Nommik & Vahtras, 1982).

Because of exchange and fixation processes the mobility of ammonium in the soil is an order of magnitude below that of nitrate (Bowen, 1973). Transfer to the root surface is by diffusion, which is the rate-limiting step in ammonium uptake. The absorbing capacity of the root/mycorrhizal complex only becomes important when transfer to the root surface is rapid (Bowen, 1981). Consequently root abundance is of primary importance in ammonium uptake, which may also be enhanced by the presence of mycorrhizae (Bledsoe & Zasoski, 1983).

Nitrate appears to be of minor importance in undisturbed forest, the ammonium:nitrate ratio being of the order 10:1 (Cole, 1981). Nitrate is an anion and as such is highly mobile under a range of soil conditions, because the anion absorption capacity of most soils is low relative to their cation exchange capacity. Once formed, nitrate is less likely than ammonium to enter into the immobilization/mineralization process, except via plant uptake, since heterotrophic microbes show a preference

Table 1. N capital values for compartments in coniferous and broadleaved ecosystems (kg/ha)  
(From Cole & Rapp, 1981; Fogel, 1980; Melillo, 1981).

	Minimum	Mean	Maximum
<i>Coniferous</i> <sup>1</sup>			
Foliage	51	120	228
Branches	18	100	242
Bole	47	176	584
Total above ground	153	396	729
Roots	12	101	422
Total tree	165	470	900
Forest floor	85	613	2260
Soil (to rooting depth)	1753	4117	7100
<i>Deciduous</i> <sup>2</sup>			
Foliage	53	84	121
Branches	20	165	666
Bole	120	208	386
Total above ground	240	497	1071
Roots	57	169	434
Total tree	389	688	1260
Forest floor	44	399	1100
Soil (to rooting depth)	1380	6142	13800

<sup>1</sup> Based on 21 sites

<sup>2</sup> Based on 20 sites

for ammonium as an N source (Jones & Richards, 1977). However, where available N concentrations are low, it seems likely that nitrate will be exploited even if it is not the preferred source. At high nitrate concentrations transport to the root surface is largely by mass flow and root absorbing capacity may influence the rate of uptake (Bowen, 1981); under such conditions mycorrhizae are unlikely to enhance uptake. At low concentrations diffusion becomes the major transfer mechanism and uptake may be improved by mycorrhizae (Bowen, 1973; Bledsoe & Zasoski, 1983).

Many vascular plants can utilize both nitrate and ammonium although one or the other may be preferentially absorbed (Driessche, 1978; Ho & Trappe, 1980). Most microbes and many mycorrhizae also appear to grow best with ammonium as their N source (Carrood, 1966; Lundberg, 1970; Paul & Juma, 1981). However, nitrate reductase activity has been demonstrated in a range of mycorrhizae and forest tree roots (Bowen, 1973; Ho & Trappe, 1980; Bledsoe & Zasoski, 1983; Buwalda *et al.*, 1983).

Bledsoe (1976) indicated that species that have evolved in a high ammonium and low nitrate environment have developed an uptake selectivity for ammonium, and vice versa, for nitrate. Considering that many forest ecosystems are N limited (Keeney, 1980; Gosz, 1981) it is strange to find a discrimination between the two main inorganic N forms. However ion-absorbing capacities and uptake selectivities determined in solution culture are unlikely to be important in the soil for the reasons already discussed. Forest trees are almost certainly opportunistic in their exploitation of available N and probably utilize whatever N is available (Wollum & Davey, 1975). That many tree species and their mycorrhizae do have a capacity to use nitrate, even when nitrate levels are usually low, tends to confirm that this is the case. An ability to use nitrate would be an advantage where N is limiting growth and also in reducing loss from the system (Ho & Trappe, 1980). The fact that nitrate reductase is a substrate-inducible enzyme (Adams & Attiwill, 1982) suggests that trees can respond to increased nitrate availability, while not having to maintain a capacity to metabolize nitrate when levels are low.

Recent work (Bowen, 1981; Bowen & Smith, 1981; Alexander, 1982) has demonstrated the ability of mycorrhizae to exploit soluble organic N compounds, the uptake of which may be important (Heal *et al.*, 1982).

### 3. Rates of nitrogen uptake

Rates of N uptake vary with site conditions, species, stage of stand development, and rate of growth (Keeney, 1980; Cole, 1981; Cole & Rapp, 1981; Gosz, 1981; Melillo, 1981; Heal *et al.*, 1982), so that values of uptake alone have little meaning (Miller, 1979).

By comparison with intensively-managed agricultural crops, N uptake by forest seems very small - approximately one-half to two-thirds of that required by a maize crop (Keeney, 1980). Cole



& Rapp (1981) give a mean annual N uptake of 55 kg/ha for 37 sites, ranging from 129 kg/ha for red alder to 2.6 kg/ha for black spruce.

Generally N uptake by forests follows the pattern temperate > boreal, deciduous broadleaved > coniferous evergreen, with the broadleaves taking up approximately twice as much as the conifers (Cole, 1981; Gosz, 1981).

This difference in uptake does not appear to result from differences in production, which is broadly similar in the two types (Gosz, 1981), but may be associated with greater rates of mineralization under broadleaved species. While natural forests may have low rates of uptake, managed stands have higher rates. The annual N uptake required to support maximum growth rate of Corsican pine was 69 kg/ha (Williams, 1983), while Cole (1981) grew Douglas fir under conditions of luxury N availability and obtained an uptake of 78 kg/ha; if ground vegetation was included total uptake was 215 kg/ha (a value approaching those of agricultural crops).

N requirement differs from N uptake. The latter (for a closed canopy system) is measured as the N increment of woody components plus N losses in litter, crown leaching and root exudation while the former is defined as the N increment of woody components plus the N needed for current foliage and fine root production. Because of internal recycling and the small amounts of N immobilized in wood, requirement may be only 8-38% of uptake (Miller, 1979). However, data from Cole & Rapp (1981) indicate that requirement can exceed 85% of uptake in temperate forest.

It is unfortunate that many studies which have assessed N uptake and requirement have failed to consider fine root turnover. Since this can represent considerably more N than above-ground litter inputs, uptake may be markedly underestimated where only above-ground litter input is measured. Failure to include fine roots in the calculations is at best inaccurate and at worst conceptually misleading. The same applies to estimates of N requirement since a large throughput of N is needed by the rapidly turned-over fine root system (Fogel & Hunt, 1983). Estimates of primary production and N requirement which include fine roots may be almost double those that are based solely on above-ground measurements (McClougherty *et al.*, 1984).

Rates of forest production and N uptake are highly correlated (Cole & Rapp, 1981), both being influenced by N availability (Cole, 1981). For optimal growth the concentration of a nutrient in the soil solution should be maintained above a certain critical value below which production is impaired (Mengel & Kirkby, 1982). This concentration is not fixed but is inversely related to the soil's buffering capacity for the nutrient in question (Mengel & Busch, 1982). For ammonium it will depend on the soil's cation exchange capacity and the rate of mineralization. Ingestad *et al.* (1981) demonstrated that relative growth rate depends upon the relative addition rate of N. It is possible to achieve both a high relative growth rate and a stable internal N concentration at a low external N concentration, so long as the rate of addition (i.e. flux) is high. The concept of a relative addition rate accords with the soil situation, where solution concentrations may be low but are maintained through cation exchange and mineralization. Mineralization rate, relative root growth rate, root morphology and mycorrhizae all influence plant N status and growth by determining the N flux available to the plant.

#### 4. Nitrogen use strategies and efficiency

Differences in N uptake between coniferous evergreens and deciduous broadleaves can be partly explained by the conifers' extended foliage retention. Deciduous species adopt the stress avoidance strategy, during adverse environmental conditions, of shedding their foliage. Evergreen coniferous species invest in stress resistance and have needles which are morphologically and physiologically adapted to withstand periods of seasonal stress. Perennial leaf retention, coupled with a high rate of photosynthesis and N retranslocation from aging foliage maximizes photosynthetic production per unit of foliar N. Photosynthetic efficiency per unit of foliar N is directly proportional to leaf longevity and photosynthetic rate, but inversely proportional to N concentration (Small, 1972 a and b; Shaver, 1981; Vitousek, 1982). Conifers maintain lower foliar N concentrations than broadleaves (Gosz, 1981) although the amount of N per unit of leaf area is actually greater because of the lower specific leaf area. Conifers therefore invest greater carbon and mineral mass per unit leaf area, but obtain an overall advantage through extended retention (Gosz, 1981). Also, conifers can concentrate N into a small area of photosynthetically active tissue, by withdrawal from older foliage (Fife & Nambiar, 1982, 1984) maximizing photosynthetic production per unit N (Schlesinger & Chabot, 1977). Such adaptations enable conifers to produce 50% more dry matter per unit N for a given leaf area, or 100% more for a given leaf weight, than broadleaved species (Cole, 1981; Cole & Rapp, 1981; Gosz, 1981).

The importance of extended needle retention is underlined by the observation that species adapted to poor sites generally retain their foliage for longer periods than species growing where N is readily available (Cole, 1981). Needle retention time also increases in a given species in response to low N availability.

In managed stands the onset of N deficiency is commonly associated with pronounced N withdrawal and the sacrificial abscission of older needles (Miller, 1981), i.e. foliage longevity is reduced. These observations are not incompatible. Natural stands are subject to comparatively stable N availability, to which growth rates and needle retention are adjusted. The supply of other

nutrients is also likely to be in balance. Managed stands are subject to greater fluctuations in N supply as a consequence of periodic fertilizer application; this may make it difficult for the relative growth rate to adjust to changes in N availability. In addition, other nutrients are commonly supplied as fertilizer in the absence of N, resulting in an imbalance of supply and the development of N deficiency. If a balanced nutrient supply is provided the relative growth rate should respond to the rate of N supply and deficiency symptoms should not appear (Ingestad, 1982).

Efficiency of N use may be inversely related to N circulation in the ecosystem. Vitousek (1982), reviewing much of the recent literature, found that the quantity of N in litterfall and N use efficiency (expressed as the ratio of litter dry weight to weight of litter N) were inversely proportional to N availability. For sites where N availability was high, N use efficiency was low, and vice versa. This observation may be explained in terms of species change; conifers are more efficient than broadleaves in their use of N and tend to be associated with sites where mineralization rates are low. Phenotypic changes within a species can also occur, e.g. Turner (1977) showed that depending on soil N availability, Douglas fir could adjust the portion of its N requirement obtained from foliar withdrawal. However, Chapin (1980) found no evidence for increased N reabsorption on poor sites compared with good sites, while both absolute and relative N withdrawal may actually be greater in species with high foliar N concentrations (Chapin & Kedrowski, 1983).

Little is known about the response of fine roots to N availability. Trees may allocate a greater proportion of resources to fine root production on poor sites, associated with a general shift in the root: shoot productivity ratio (Keynes & Grier, 1981). Such a shift would be accompanied by a change in litter inputs and possibly in the pattern of N cycling. Standing-crop or productivity comparisons between stands growing on different sites may indicate differences incorrectly if only the above-ground components are considered.

## 5. Changes in nitrogen uptake during stand development

N uptake changes with stand development (Kazimirov & Morozova, 1973; Attiwill, 1981; Miller, 1981). Initially, cycling is dominated by uptake, which must continually increase to meet the demands of growth and development. At this stage leaf area and twig weight are continually increasing; each year the new foliage weight exceeds that of the previous year. As a result it has usually been thought that virtually none of a tree's N requirement can be met by translocation. However, Fife & Nambiar (1982, 1984) demonstrated that 48% of the N required for current shoot production in 3-year-old radiata pine could have come from young needles formed during the preceding spring. Significant retranslocation also occurred from needles only 3 months after their initiation. While such retranslocation could not be expected to support a continued increase in tree size in the absence of uptake, it could clearly be important in satisfying N demand when conditions are not conducive to uptake from the soil.

With time the forest floor begins to form, the annual N release from litterfall being a function of tree size a year or more previously (Miller, 1981). Since the crowns are still small, and do not fully occupy the site, capture of atmospheric input is low while its retention in the tree biomass may be low because of limited root system development and competing ground vegetation. Virtually all the trees' uptake demand must be met by the soil, and N concentration and replenishment in the soil solution is critical to stand development at this stage.

Maximum leaf area (or leaf biomass) is achieved just before canopy closure. It then declines slightly (because of shading) and finally stabilizes to remain more or less constant (Bray & Gorham, 1964; Rodin & Bazilevich, 1967; Vitousek, 1982). Leaf litterfall also becomes constant (Gessel & Turner, 1976) and the forest floor may attain a steady state, depending on the rate of decomposition. Uptake remains fairly constant since the only increase is in N immobilization in woody components, where the concentration of N is very low (Vitousek, 1982).

A large proportion of nutrient requirements can now be met by internal recycling. Increased capture and retention of atmospheric inputs can actually meet the demand for certain nutrients, but not N or P. The soil is replaced by the forest floor as the main zone of uptake, and this is associated with a shift in fine root abundance from the soil to the forest floor layers (Vogt *et al.*, 1981). However, the soil must continue to supply some N (Miller, 1981).

Where N is especially limiting, low N concentrations in the litter may lead to a decline in the decomposition rate and an accumulation of the forest floor. This implies N immobilization, which may result in N deficiency and progressive deterioration in the nutritional condition of mature stands (Williams, 1983).

N uptake will therefore increase progressively until canopy closure when it stabilizes, slightly below its maximum value, as internal cycling mechanisms begin to operate. This situation may continue (Miller, 1981) or uptake may eventually decline as the stand becomes overmature (Kazimirov & Morozova, 1973; Grier *et al.*, 1974; Gosz, 1981).

## III. External nitrogen inputs into forest ecosystems

### 1. Atmospheric nitrogen additions

The transport of atmospheric N to vegetation surfaces and to the soil occurs as a result of two distinct processes, dry deposition and wet deposition.

Wet deposition is mediated by precipitation (rain or snow) and measurements of N input by this mechanism exist for most geographical areas (Soderlund & Svensson, 1976; Soderlund, 1981). The quantity of N added by wet deposition depends upon the amount of precipitation and the concentration of N compounds in that precipitation. Areas with low precipitation normally exhibit higher concentrations of N, although the total N added is less than in high rainfall areas (Soderlund, 1981). Incorporation of N compounds into rain occurs within clouds or during drop descent. In Europe wet deposition returns annually 1-6 kg/ha of nitrate N and 1-5 kg/ha of ammonium N (Bottger *et al.*, 1978). Maximum nitrate values occur in or near industrial areas associated with high N oxide concentration (Henderson & Harris, 1975; Melillo, 1981), while high ammonium concentrations are associated with agricultural activity and particularly with large numbers of livestock (Soderlund & Svensson, 1976).

Dry deposition is less clearly understood than wet deposition and involves the trapping on plant surfaces of wet particles (mist and rainfall), dry particles (dust) and gases (Miller, 1984). Transfer to plant surfaces and subsequent trapping can involve gravitational settling, turbulent transfers, diffusion and impaction (Miller, 1979; Soderlund, 1981). In the case of particles dry deposition provides a net input after allowing for resuspension in the atmosphere which can occur from the canopy surface (Soderlund, 1981; Miller, 1984).

The presence of a vegetation canopy increases dry deposition (Melillo, 1981), which is greater for forest than other vegetation types (Chamberlain, 1975). This is because the aerodynamic roughness of a forest canopy is considerably greater than that of other vegetation surfaces. It is influenced by gross canopy features such as height and foliage density (Gorham *et al.*, 1979) and surface microproperties such as leaf hairs (Wedding *et al.*, 1977). Turbulent air flow increases the momentum of particles, enabling them to penetrate the boundary layer of still air around the leaf and impact on the surface (Chamberlain, 1975). Without turbulent air flow, particles are more likely to be swept past an obstruction in a gentle wind (Miller, 1984). Turbulent air flow also increases the exchange between the air within the canopy and the atmosphere outside it, thereby enhancing the supply of particles and gases in the canopy zone (Miller, 1984).

Fog and mist droplets behave as large particles (Soderlund, 1981) and are less likely to become resuspended than dry aerosols. Moreover, element concentrations in mist, fog or fine rain exceed those of rainfall (Lovett *et al.*, 1982). Consequently it has been suggested that much of the 'dry' deposition occurs as mist, fog and fine rain (Miller, 1984).

Gaseous deposition is at its most important when surfaces are moist, since the majority of atmospheric N gases are highly soluble. Surface moisture may partly explain ammonia absorption by soils (Paul, 1976) and by acid moss vegetation (Tamm, 1953).

Because dry deposition is difficult to measure directly, the amounts of N contributed are uncertain. For beech forest, Mayer & Ulrich (1974) found an annual input of 5.8 kg/ha by dry deposition compared with 22.6 kg/ha in bulk precipitation. Nilhgard (1970) found 0.7 kg/ha compared with 8.2 kg/ha, again for beech. Annual bulk precipitation input of N in Europe ranges around 5 kg/ha, e.g. Miller (1979) gives a value of 5 kg/ha, Heal *et al.* (1982) 6 kg/ha and Tamm (1982) 4 kg/ha. For 36 IBP sites the mean annual N input in bulk precipitation was 9.8 kg/ha, the range being 1.0-22.8 kg/ha (Cole & Rapp, 1981).

Evidence suggests that conifers are considerably more efficient than broadleaves at trapping aerosols. Conifers generally have a greater leaf area resulting in greater interception, 3-6 mm of rain being required to wet conifer foliage compared with 0.5-2.0 mm for broadleaves (Larcher, 1975). This high interception is accompanied by greater dry deposition (Schlesinger & Reiners, 1974; Mayer & Ulrich, 1978). These factors, coupled with autumnal foliage loss by many broadleaves, may result in significantly greater atmospheric input in coniferous systems, an important consideration for poor sites (Gosz, 1981).

### 2. Biological nitrogen fixation

Biological N fixation is the process by which atmospheric  $N_2$  is converted to  $NH_3$  by the enzyme nitrogenase (Stewart, 1982). Development of the acetylene reduction assay, a rapid technique for assessing N fixation (Hardy *et al.*, 1973; McNabb & Geist, 1979), has led to considerable research on N fixation in a range of natural and managed systems. Much of this research has been reviewed by Nutman (1975), Jones (1978), Gordon *et al.* (1979), Smittle (1979), Granhall & Lindberg (1980), Granhall (1981), Waughman *et al.* (1981), Stewart (1982), and Gordon & Wheeler (1983). Biochemical aspects of N fixation and the acetylene reduction assay have been dealt with by Hardy & Burns (1968), Hardy *et al.* (1973), Stewart (1982), and Dixon & Wheeler (1983).

Biological N fixation is carried out by a number of heterotrophic organisms and autotrophic blue-green algae. These organisms may occur as symbiotic associations or free-living forms. Symbiotic N fixation is associated with both leguminous and non-leguminous plants and lichens.

Legumes (Leguminosae) comprise 748 genera (distributed among three sub-families) of some 13 000 species (Alexander, 1977; Allen & Allen, 1981). Legumes form N-fixing root nodules with bacteria of the genus *Rhizobium* and are undoubtedly the most important plant group concerned in symbiotic N fixation worldwide (Allen & Allen, 1981; Havelka *et al.*, 1982). Annual rates of fixation associated with legumes vary widely, from less than 1 to more than 500 kg/ha (Nutman, 1976; Lawrie, 1981). High rates are associated with the herbaceous forms, lower rates with the woody forms. In forest ecosystems most of the naturally occurring legumes are woody perennials, most of which are restricted to the tropics and southern hemisphere, although several species occur in North American forests (Pritchett, 1979). Although N-fixation rates associated with these woody types tend to be low, they may still influence N cycling in natural systems (Turvey & Smethurst, 1980; Adams & Attiwill, 1984).

Although non-leguminous plants may form symbiotic associations with a range of N-fixing microbes (Bond, 1983) the most important in forest systems are those forming *Alnus*-type root nodules with bacteria of the genus *Frankia*. Such plants are commonly termed actinorhizal (Stewart, 1982) and so far 20 genera, with 194 species, have been shown to possess nodules (Bond, 1983). Some of the best known are *Alnus*, *Casuarina*, *Ceanothus* and *Myrica*. Annual amounts of N fixed by actinorhizal associations vary widely, from 0.1 to 320 kg/ha, but are generally as good as and often substantially better than for woody leguminous types (Stewart, 1982). Unlike the legumes, actinorhizal species are important in both hemispheres, with 12 genera represented in the northern hemisphere (Bond, 1983).

Lichens are an association between a fungus (usually an ascomycete) and an alga (commonly a green alga, less commonly a blue-green alga and rarely both). Only the blue-green associations can fix N and these account for only 7% of lichen species (Bond, 1983). They are undoubtedly important for N fixation in tundra and boreal forest (Granhall & Lindberg, 1978; Cleve & Alexander, 1981) but have also been shown to contribute small quantities of N, 3-4 kg/ha annually, to Douglas fir forest (Denison, 1979).

Environmental factors influencing symbiotic N fixation in plants have been reviewed by Havelka *et al.* (1982), and Dixon & Wheeler (1983): virtually all research has focused on the legume/rhizobium association. N fixation is an energy-demanding process so that rates of nodule fixation depend heavily on the supply of photosynthate. Consequently it is influenced by the rate of photosynthesis, light intensity, photosynthetic area and photosynthate allocation to other competitive sinks. Any factor which influences photosynthesis or plant growth is likely to influence nodule fixation. Soil pH is important; nodule formation in legumes are inhibited when pH is less than 4.5-5.5. Certain actinorhizal species such as *Alnus* and *Myrica* produce nodules when the pH is less than 4.5, but rates of N fixation are reduced. High internal ammonium concentrations inhibit fixation but are unlikely to be important so long as the plant acts as a sink for fixed N. High external ammonium concentrations also inhibit fixation.

The use of symbiotic N-fixing associations to supply N in managed forests has recently received considerable attention (Gordon *et al.*, 1979; Turvey & Smethurst, 1980; Domingo, 1983; Gadgil, 1983; Gordon, 1983; Mikola *et al.*, 1983; Tarrant, 1983; Turvey & Smethurst, 1983). There is substantial experimental evidence that N-fixing plants can be beneficial in managed forests but this has not resulted in their widespread use. Such management inertia is caused by a variety of factors which include: low cost and flexibility of use of inorganic N fertilizers, lack of evidence demonstrating economic benefits, and absence of methods for the concurrent establishment of N-fixing plants and tree seedlings (Turvey & Smethurst, 1983). The likely advantages and disadvantages of symbiotic biological N fixation as a silvicultural tool were summarized by Gordon (1983):

Advantages (relative to inorganic N fertilizers):

- Provides a regular supply of available N over a long period.
- Leaching or volatilization losses less likely.
- Less likely to cause public concern about 'chemical' use.
- A source of organic matter.
- Particularly attractive to landowners who have difficulty in obtaining N fertilizer or who lack the technology to apply it.

Disadvantages:

- Use is limited by lack of knowledge of the biology and silviculture of N-fixing species.
- Likely to be more expensive per unit of applied N.
- Takes longer to produce fertility increases.
- A possible source of vegetative competition for the main crop species.
- Managerially more complex.

In forests where symbiotic N fixation is restricted or absent, N may still be fixed by free-living heterotrophs and autotrophic blue-green algae (Granhall & Lindberg, 1978). The heterotrophs include actinomycetes, fungi and bacteria (both aerobic and anaerobic). Blue-green algae may be crust-forming, as in some Swedish forests (Waughman *et al.*, 1981) or associated with mosses



(Granhall & Selander, 1973; Weber & Cleve, 1981). They are important N fixers in tundra and boreal forest, while heterotrophic fixation dominates in temperate forest (Granhall, 1981).

Free-living N fixation is influenced by several environmental factors. It is positively correlated with soil moisture and temperature; it has a  $Q_{10}$  of 3-6 and an optimum around 30°C, and is inhibited by dry conditions and extreme cold (Jordan *et al.*, 1978; Stewart *et al.*, 1978; Jaeger & Werner, 1981). Oxygen can inhibit nitrogenase but most species have effective enzyme protection systems so that the influence of oxygen varies (Alexander, 1977). Soil pH can explain 34% of variation in nitrogenase activity; the optimum is around pH 7; fixation declines with increasing acidity but can still occur at pH 4 (Granhall & Lindberg, 1978; Waughman & Bellamy, 1980). Free-living N fixation may be positively influenced by the amount of calcium, potassium and molybdenum in the soil, while high ammonium or aluminium contents are detrimental (Hardy *et al.*, 1973; Granhall & Lindberg, 1978; Waughman & Bellamy, 1980). Since free-living N fixers cannot depend on a host for carbohydrate supply, fixation in forest ecosystems is probably controlled mainly by the availability of carbohydrate (Granhall, 1981), and it is stimulated by the addition of available carbohydrate (Waughman *et al.*, 1981). N fixation in the rhizosphere may depend upon carbon-rich exudates (Barber & Lynch, 1977; Bond, 1983).

Non-symbiotic N fixation can be detected in most components of forest ecosystems (Melillo, 1981). Phyllosphere fixation has been detected by a number of workers (Richards & Voigt, 1965; Jones, 1978; Sucoff, 1979). Results obtained by Jones suggested important rates of canopy fixation but later revision of these estimates (Sucoff, 1979) and the findings of other researchers suggest that input is small (Granhall & Lindberg, 1978). For 51 woody species the maximum annual fixation in the canopy was 0.2 kg/ha (Sucoff, 1979) and it seems unlikely that values exceed the revised values of Jones (2.4 kg/ha).

N fixation is also associated with living and dead woody material, particularly stems (Granhall & Lindberg, 1978; Waughman *et al.*, 1981; Spano *et al.*, 1982). Amounts fixed are invariably small but they may be important where woody litter constitutes the bulk of the forest floor (Graham & Cromack, 1982). Forest floor N fixation is particularly associated with the F layer (Waughman *et al.*, 1981) which, in relative terms, is an important site for N fixation (O'Connell *et al.*, 1979).

Stimulation of N fixation in the rhizosphere seems to be well known (Rambelli, 1973; Richards, 1973; Dobereiner, 1974; Barber & Lynch, 1977). Fixation is often associated with mycorrhizal roots although bacteria are possibly responsible (Richards & Voigt, 1964; Jurgensen & Davey, 1971; Silvester & Bennet, 1973).

Annual fixation rates of non-symbiotic N vary but are probably in the range 1-12 kg/ha with many forests fixing less than 10 kg/ha (Jones, 1978; Granhall & Lindberg, 1980; Granhall, 1981; Waughman, 1981; Waughman *et al.*, 1981; Tamm, 1982). Although absolute amounts are small they can represent 5-10% of the N annually cycled through vegetation (Paul, 1978). The importance of biologically-fixed N may be greater than the amount of it would suggest, because it is released as diverse organic compounds which may stimulate other microbial processes. In particular the decomposition of woody litter with very high C : N ratios is linked with N-fixing bacteria which provide an N source for basidiomycetes attacking the N-poor substrate (Sunderstrom & Huss, 1975; Silvester *et al.*, 1982; Spano *et al.*, 1982). While it may be possible to stimulate non-symbiotic N fixation in certain agricultural systems (Stewart, 1982) it is unlikely that this could ever become practical in managed forest.

### 3. Geological nitrogen inputs

Weathering of primary geological deposits is unimportant as an N input to forest ecosystems. However, the weathering of certain organic-rich secondary deposits can be important in a few restricted localities (Woodmansee *et al.*, 1979; Reiners, 1981).

### 4. Nitrogen fertilizers

Since N is the element most frequently limiting to forest production it is commonly applied as fertilizer in managed forests, where fertilizers may represent the principal N input. Forms and application rates of N fertilizers vary widely and will not be considered here.

## IV. Nitrogen losses and budgets

### 1. Mechanisms

The principal mechanisms for N loss from forested ecosystems are denitrification, ammonia volatilization and leaching.

Denitrification has been the subject of several recent and comprehensive review articles (Focht & Verstraete, 1977; Knowles, 1981, 1982; Firestone, 1982). It is the dissimilatory reduction of one

or both of the ionic N oxides (nitrate and nitrite) to gaseous N oxides which may be further reduced to molecular  $N_2$ . All gaseous forms are subject to loss. The reactions involved are catalysed by a wide range of mainly heterotrophic bacteria. Five environmental factors positively (+) or negatively (-) influence denitrification rates: oxygen (-); organic carbon (+); amount of substrate (+); pH (+); and temperature (+). Oxygen is the most critical since denitrification only occurs under anaerobic conditions, consequently saturated or water-logged soils are likely to support denitrification, although it may also occur in well-aerated soils in anaerobic sites within soil aggregates (Smith, 1980).

One would expect significant denitrification in anoxic, warm, neutral soils high in organic matter and nitrate (Keeney, 1980). Little information exists on denitrification in forests but it is likely to occur, at least at low rates (Wollum & Davey, 1975). The large amounts of soluble organic matter in forest floors would favour denitrification, but aeration tends to be good and pH is normally well below optimum. The low rate of nitrate production in most forests should also restrict denitrification losses.

Despite these factors several workers e.g. Melillo (1981) have detected significant levels of denitrification in forests. Bormann & Likens (1979) found that 19% of N entering a northern hardwood forest was lost through denitrification, while in another deciduous forest 27 kg/ha of N was lost as gases (Melillo *et al.*, 1981).

The subject of ammonia volatilization, which occurs when ammonium is converted to gaseous ammonia, has been reviewed in detail by Freney *et al.* (1981), and Nelson (1982). Unlike denitrification the process is not biologically mediated but is still influenced both positively (+) and negatively (-) by four environmental factors: pH (+); temperature (+); amount of substrate (+); and soil buffering capacity (-). The conversion of ammonium to ammonia generates hydrogen ions which cause acidification in poorly-buffered soil, and since only 0.1% of ammonium + ammonia occurs as ammonia when pH is less than 6 (Wollum & Davey, 1975), this acidification significantly reduces N loss. Because ammonium rarely accumulates in unmanaged forest, and soil pH is normally less than pH 6, loss by volatilization is negligible.

N transport in soils has been considered in detail by Nielsen *et al.* (1982). As ammonium is held by the soil cation exchange sites, its potential loss by leaching is low in undisturbed forest. Since nitrate is not held by the soil in any substantial quantity and is less likely than ammonium to enter the immobilization/mineralization process, it is subject to loss in downward-percolating water together with a loss of balancing cations (Robertson, 1982).

## 2. Factors controlling nitrogen loss

Perhaps the most important control on N loss from forests is plant uptake (Cronan, 1980b; Vitousek *et al.*, 1982). In addition to this, the soil retains N in the form of ammonium, and high rates of nitrification are prevented in many forest ecosystems. Significant N loss normally only occurs where high nitrate concentrations build up in the absence of effective plant uptake (Bormann *et al.*, 1974). Because of these N-conserving mechanisms, losses of N determined for a variety of forest ecosystems have been shown to be small, Feller (1977), Miller *et al.* (1979), Rapp *et al.* (1979), Cronan (1980a), Keeney (1980), Sollins *et al.* (1980), and Sollins & McCorison (1981). Reported annual values range from 0.1 to 4 kg/ha (Cole & Rapp, 1981; Gosz, 1981) although higher values do occur (Melillo, 1981).

A large number of budgetary studies indicate that N inputs exceed N losses, often by a factor of two (Gorham *et al.*, 1979; Gosz, 1981; Melillo, 1981; Reiners, 1981; Tamm, 1982). For 36 IBP sites the net balance of N was an annual increment of 4.5 kg/ha, with only one site showing a deficit (Cole & Rapp, 1981).

## 3. Effects of management on nitrogen loss

Two operations may result in an increased net N loss from forest ecosystems: cultivation and harvesting. The latter has received most attention and will be considered first.

Substantial N losses as a result of timber harvesting are only likely where significant nitrate production occurs (Vitousek & Melillo, 1979; Matson & Vitousek, 1981; Vitousek, 1982; Vitousek *et al.*, 1982). Most of the following is based directly on the findings of these workers. In undisturbed forest the rate of N uptake equals or slightly exceeds the rate of N mineralization, while losses are negligible. Timber harvesting removes the sink for N uptake and may increase the rate of mineralization by increasing soil temperature and moisture, increasing the frequency and intensity of wetting and drying cycles in the forest floor, increasing the mineralizable substrate, and decreasing resource competition between heterotrophs and mycorrhizae (Vitousek *et al.*, 1982). As a result, soil ammonium concentration may increase and, in neutral to alkaline soils, ammonia volatilization could occur. Alternatively, nitrification may occur with subsequent loss through leaching or denitrification.

On N-deficient sites the quantities of N cycled between the vegetation and the soil are low, N mineralization rates are correspondingly low and the C : N ratios of the litter and the forest floor are high. Such sites have a large capacity to immobilize N, and losses are unlikely to increase after harvesting. On better sites, where N circulation and mineralization rates are greater, soil mineral N

content may still be small because of plant and microbial uptake. Nitrifying populations will be low, so that any disturbance will lead to increased ammonium availability but nitrification will lag behind as the nitrifying populations build up. On the most fertile sites N circulation and mineralization rates are high, C : N ratios are low and nitrifying populations are likely to be well established as a result of greater mineral N availability. Timber harvesting should lead to an immediate increase in net mineralization and nitrification.

Loss of N is likely to be strongly influenced by the rate of revegetation. On poorer sites it will be slow, thus while the rate of N loss may be low it may continue over a prolonged period. On fertile sites revegetation will be rapid, so that N loss is likely to peak soon after harvesting, followed by a rapid decline.

Such findings have important implications for forest management. On poor sites N losses after harvesting are unlikely to be significant, especially if woody logging residues are left on the site where they would serve to immobilize N. On better sites N losses may occur but will be of short duration, and again the retention of woody residues will probably reduce loss. Whole-tree harvesting or the removal of woody residues are likely to increase immobilization. Where revegetation is rapid, early weed control will exacerbate loss; if weed control is required for the successful establishment of the next crop it should be restricted to selective control around the planted trees, rather than an over-all treatment. Silvicultural systems which do not drastically reduce plant uptake, or only do so progressively, i.e. selection methods, shelterwoods, underplanting and coppice, are unlikely to be associated with N loss.

N removal by conventional harvesting methods is minimal and may not greatly exceed N accretion during the rotation. However, whole-tree harvesting may increase N removal by as much as 288% (Kimmins, 1977). It may have a substantial effect on poorer sites, although loss could be offset by increased fertilizer usage.

Cultivation may be required on previously unforested land to aid plantation establishment or it may follow harvesting for the establishment of the next rotation. In both cases the effects of cultivation are to disturb the soil and provide a weed-free area for seedling establishment. Virtually any form of severe soil disturbance, such as ploughing, results in increased rates of mineralization (Powlson, 1980) which, because of the simultaneous removal of vegetation may lead to N loss. The factors controlling loss are likely to be similar to those already discussed for harvesting.

The use of N fertilizers may lead to an increase in N export from a forest, but the net result will be an increase in the N capital of the system. A net loss N has been shown to occur on deep peat sites after fertilization with ground mineral phosphate, which appears to stimulate native N mineralization (Carey *et al.*, 1981; Malcolm & Cuttle, 1984).

## V. Internal nitrogen cycling

### 1. Introduction

External inputs and losses of N have already been considered; the internal cycling of N will be dealt with here. Within an ecosystem N moves among three compartments; the vegetation; the forest floor plus organic soil layers; and the sub-soil. Trees take up available N from the forest floor and soil and release N through litterfall, throughfall, root death and root exudation. Release of organically-bound N occurs by decomposition and mineralization in the forest floor.

### 2. Throughfall and stemflow

As rain passes through a canopy its chemical nature is altered by foliar leaching and adsorption (Feller, 1977; Turkey, 1970, 1980; Olson *et al.*, 1981), enrichment from accumulated deposition (Soderlund, 1981; Parker, 1983), cation exchange (Eaton *et al.*, 1973) and nutrient uptake and release by epiphytes and the phylloplane microflora (Ruinen, 1974; Lang *et al.*, 1976; Parker, 1983). Because of differences in these variables throughfall characteristics vary with season, quantity and nature of precipitation, foliar element concentrations and tree species (Miller, 1979).

The cycling of N as throughfall seems to be quantitatively unimportant; most studies indicate a decrease in the amount of N, or a slight increase, relative to unaffected rainfall (Zimka & Stachurski, 1979; Luxmoore *et al.*, 1981; Olson *et al.*, 1981; Ostman & Weaver, 1982; Ryan & Bormann, 1982). However N concentrations increase because of evaporation (Parker, 1983). The quality of rain is changed by contact with a canopy. Most obvious is the increase in organic N compounds (Nykqvist, 1963; Verry & Timmons, 1977; Olson *et al.*, 1981) due to foliar leaching, foliar exudates, and decomposition products from epiphytic microbes (Mahendrappa & Ogden, 1973). The presence of such compounds may act as a growth stimulus for saprophytic organisms in the forest floor (Clarholm & Rosswall, 1980).

A portion of the rain intercepted by a canopy is directed towards the stem and becomes stemflow. Amounts are influenced by crown structure and bark characteristics (Ford & Deans,



1978), being greater for smooth-barked species (Parker, 1983). Stemflow transports less material to the forest floor than throughfall, amounting to 1-20% (mean 12%) of the throughfall flux (Parker, 1983), the absolute amounts of N being less than in rainfall (Olson *et al.*, 1981). However, element concentrations in stemflow exceed those in throughfall by an order of magnitude, and pH is invariably lower (Parker, 1983). The redistribution of rainfall as throughfall and stemflow (Ford & Deans, 1978) is potentially important; it may lead to spatial differences in a number of forest floor, soil and plant growth processes.

### 3. Root exudation

Assessing the importance of root exudates to the cycling of N is extremely difficult, since both composition and quality are influenced by plant age, plant nutrient status, light, temperature, moisture and rhizosphere microbes (Bowen & Theodorou, 1973; Rambelli, 1973). In addition, the presence of mycorrhizae may cause increased exudation (Reid *et al.*, 1983). Exudates cannot be collected without altering the root environment and therefore exudation (e.g. Smith, 1970) so that it is difficult to extrapolate results to the field.

Root exudates contain N mainly as amino acids (Smith, 1976). The N may amount to 0.8-4 kg/ha annually (Smith, 1976; Harris *et al.*, 1979). Although these are small amounts, such N is highly labile and the stimulating effect of specific amino acids on the rhizosphere may be important. Root exudates may support virtually all the bacteria and associated food chains in forest soils by providing a source of readily-metabolizable carbon. Where carbon availability is limiting, a large portion of the soil biomass may be either dead or in a state of arrested metabolism. Humic substances are unlikely to be an energy source because of their long half-life, so that continuous activity is only likely in the rhizosphere (Barber & Lynch, 1977).

### 4. Litter inputs

#### (a) Introduction

The formation of litter is a first step in the recycling of N to plants, and in forests it is the dominant pathway for supplying carbon and N to the soil systems. Reviews by Bray & Gorham (1964) and Rodin & Bazilevich (1967) cover most of the earlier literature while much of the recent material is included in a synopsis by Staaf & Berg (1981). In addition Cole & Rapp (1981) present a synthesis of IBP data.

#### (b) Above-ground input

Rates of litter production and N return are broadly proportional to primary productivity (Bray & Gorham, Rodin & Bazilevich, 1967; Miller, 1979). Foliage accounts for most of the N returned through litterfall (Gosz, 1981; Melillo, 1981). Up to 83% of the N returned annually to the forest floor is through litterfall (Cole & Rapp, 1981). Primary production is similar for conifers and broadleaves with litterfall being slightly greater beneath the conifers, but N return is greater under broadleaves because of higher N concentrations in the litter. For temperate deciduous broadleaves, 60 kg/ha of N are returned annually in litterfall while only 36 kg/ha are returned under temperate conifers (Cole & Rapp, 1981).

Deciduous species exhibit a marked increase in input before the onset of cold or dry seasonal conditions. Evergreen conifers in temperate and boreal regions also exhibit seasonal variation in leaf litter input, with maximum amounts and minimum N concentrations before the start of adverse seasonal conditions (Lee & Correll, 1978; Bares & Wali, 1979). Reproductive structures also exhibit seasonality and may have high N concentrations (Melillo, 1981); the input of pollen in early summer when conditions are suitable for active decay may be a useful source of N in temperate coniferous forest (Stark, 1972).

The input of large woody components does not follow a seasonal pattern. The quantity and proportion of woody litter increases erratically throughout the life of a stand (Gessel & Turner, 1976), related to damaging events such as high wind or heavy snow (Staff & Berg, 1981). During periods when the proportion of woody litter is high, total N returns are also high because of the large mass, but the mean N concentration of the litter is considerably reduced (Gessel & Turner, 1976). There is considerable spatial variation in the input of large woody components (Foster & Lang, 1982; Graham & Cromack, 1982).

#### (c) Below-ground input rates

Early studies, such as those reviewed by Rodin & Brazilevich (1967), appear to have greatly underestimated the importance of below-ground litter input. Fine root biomass ranges from 1 to 12.6 t/ha with turnover accounting for 63-77% of primary production (Harris *et al.*, 1979; Agren *et al.*,

1980; Fogel, 1983). Turnover of fine roots is frequently 90% of the standing crop (Fogel, 1980), resulting in an organic matter input of 2-5 times that from above-ground litterfall, equivalent to an N return 2 times greater (Henderson & Harris, 1975; Wells & Jorgensen, 1975).

Most research seems to indicate that fine root growth and death occurs independently of shoot growth, temporal variation being largely a result of environmental changes. Growth seems to take place where and when soil moisture and temperature conditions are favourable. Poor growth and death of fine roots are commonly associated with soil moisture stress and low temperature (Deans, 1979; Persson, 1980; Nambiar, 1983). However, fine roots are carbon sinks and must receive carbohydrate produced during photosynthesis. Roots may require 57% of a tree's carbohydrate production (Agren *et al.*, 1980) *although temporary storage permits root growth to be asynchronous with the production of carbohydrate.*

(d) Short circuits

Primary consumption, particularly of foliage, can influence litter formation by altering the timing of input, influencing the general condition of the plant, and removing N to the primary consumer food chain (Staaf & Berg, 1981).

The feeding activities of defoliating insects can have ecosystem-level consequences as a factor regulating biogeochemistry in certain systems (Swank *et al.*, 1981). Defoliation results in an input of frass and foliage debris plus leaching of elements from the damaged canopy, which may stimulate decomposition and enhance nutrient availability (Mattson & Addy, 1975; Kitchell *et al.*, 1979). Where N concentrations in litter are low, forest floor accumulation and N immobilization may occur (Williams, 1983). Under such conditions defoliation could stimulate turnover and production. Swank *et al.* (1981) have reported increased nitrate loss from broadleaved ecosystems that are suffering chronic defoliation, associated with increased soil respiration, mineralization and above-ground net primary production.

While the consumption of vegetation by large herbivores in natural and managed grasslands has important implications for N cycling, its significance in forest ecosystems is probably limited. However, grazing may be of considerable importance in agroforestry schemes where trees are grown at wide spacings, allowing a pasture sward to be grazed by sheep or cattle. Grazing can accelerate the rate of N cycling and maintain a high concentration of available N (Floate, 1981) which could have a major positive influence on early tree growth when all of a tree's N demand must be met by the soil (Miller, 1981). Such an influence has been noted in New Zealand (Sutton, 1985, personal communication) but it is likely to vary considerably depending on the initial state of soil and vegetation, climate, animal agent and the temporal and spatial distribution of both vegetation and animals (Floate, 1981).

## 5. Cycling of nitrogen within the tree

In addition to cycling between plants and the soil, N is also cycled between plant parts. This is best documented for foliage (Viro, 1955). In evergreen species it involves the mobilization and translocation of N from older foliage to younger foliage, stem, branches and roots, while deciduous trees can only translocate to perennial organs. Trees may also withdraw N, prior to cell death, as cells pass from the cambium to form xylem tissue, thereby preventing long-term immobilization (Miller, 1981).

Translocation of N from aging or abscising tissue gives the tree an energy advantage if the N withdrawn is stored in the organic form (Staaf & Berg, 1981), and reduces the potential for loss through leaching or immobilization. Additionally it conveys a degree of nutritional independence from the soil when new growth commences in spring, at a time when N availability may be low. N withdrawal is associated with the simultaneous translocation of carbohydrates and of other elements (Chapin & Kedrowski, 1983). On breakdown the mobile fraction can be withdrawn and stored (Miller, 1981), or used to meet the demands of new tissue production (Fife & Nambiar, 1982, 1984).

Deciduous species translocate significant quantities of N prior to foliage abscission, e.g. 78% for chestnut oak (Ostman & Weaver, 1982), 90% for tamarack (Cole, 1981), 33-36% for northern hardwoods (Ryan & Bormann, 1981), and 70% for eastern deciduous forest (Luxmoore *et al.*, 1981). Coniferous evergreens also exhibit a marked withdrawal of N, e.g. for loblolly pine, 39% (Switzer & Nelson, 1972), for Scots pine, 77% (Stachurski & Zimka, 1975) or 85% (Viro, 1955). However, in evergreen species most withdrawal and retranslocation is not associated with tissue death but is the redeployment of N accumulated during periods of inactive growth or high N availability (Miller, 1979). This stored N can be mobilized to meet demands for new tissue production in conjunction with N uptake, or when N availability in the soil is low. In young radiata pine 48% of the N required for new foliage production may come from needles which are only one year old (Fife & Nambiar, 1982).

It has been suggested that conifers as a group depend less on translocation of N than deciduous species (Attiwill, 1981; Cole, 1981). Cole & Rapp (1981) indicated that some 30% of broadleaved N requirement is met by translocation from senescing foliage while there is little or no translocation in conifers, in which N uptake is generally equal to requirements. Luxmoore *et al.* (1981) found less

translocation from conifer foliage than from broadleaved on the same site. These views are clearly in disagreement with the findings mentioned above and may in part arise from a failure to recognize that considerable translocation occurs in conifers without tissue death.

Many workers have suggested that N withdrawal from abscising foliage and dependence on within-tree cycling are greater on poorer sites (Gosz, 1981; Vitousek, 1982). Stachurski & Zimka (1975) demonstrated that on an N-rich alder site, oak and hornbeam withdrew only 14% of foliar N while 68% was withdrawn by the same species on a poor site (where it was associated with pine). Lamb (1975) showed that N withdrawal from needles of radiata pine was greater on infertile than on fertile sites. One would therefore expect low N concentrations in the litter of trees growing on infertile sites, which is a common observation (Mahendrappa & Weetman, 1973; Florence & Chuong, 1974; Lamb & Florence, 1975; Miller & Miller, 1976). However, it is widely recognised that foliar N concentrations can be indicative of both tree N status and N availability and that these are depressed on poor sites (Miller, 1982). Thus low N concentrations in the litter on poor sites may, at least in part, result from low foliar N concentrations rather than indicating increased withdrawal. Fife & Nambiar (1984) showed that young, fast growing radiata pine depends heavily on N retranslocation even when foliar N concentrations are high. Chapin (1980) and Chapin & Kedrowski (1983) in comprehensive reviews of the available literature found an absolutely and proportionally greater reabsorption of N in species where foliar N concentrations were high. They proposed that the efficient use of N is a strategy shown by many plants and not one restricted to poor sites; low N concentrations in litter for species on poor sites reflect low foliar N concentrations and greater dilution with structural material rather than greater relative withdrawal.

## 6. Nitrogen cycling and ecosystem development

Where the available N capital of a site is high, N uptake and net primary production will be corresponding high (Cole, 1981) as will litter input, since this is positively correlated with primary productivity (Bray & Gorham, 1964). High N availability is normally reflected in high foliar N concentrations (Miller, 1982) which in turn result in high litter N concentrations (Chapin & Kedrowski, 1983) and a large N return to the forest floor (Vitousek *et al.*, 1982).

High litter N concentrations (low C : N ratios) favour rapid decomposition and mineralization (see section VI.3). Also, the production of polyphenols, which are commonly produced in the leaves of plants subjected to environmental stress (Puritch, 1977; Dell & McComb, 1978), is likely to be low. Polyphenols are produced in cell vacuoles and released by autolysis at senescence. They have a tanning effect on plant proteins and microbial enzymes, that results in complexes which are highly resistant to microbial attack. The degree of tanning undergone by leaf proteins determines their subsequent rate of decay (Davies *et al.*, 1964). The diversity and quantity of polyphenol production increases as site fertility decreases (Coulsen *et al.*, 1960; Davies *et al.*, 1964; Davies, 1971).

Calcium causes polyphenols to polymerize, which renders them inactive, consequently the degree of tanning caused by a given concentration of polyphenols is much greater on an acid site than on a base-rich one (Davies, 1971).

High N concentrations and low polyphenol concentrations in decomposing litter result in rapid N release which in turn leads to high available N contents. Under these conditions heterotrophic competition for ammonium will be less intense than where N availability is low and nitrifying populations may be large (Vitousek *et al.*, 1982) giving high nitrate production. Large quantities of N are then cycled between the vegetation and the soil.

Sites with high N availability are commonly associated with base-rich conditions, on soils which have a large capacity to neutralize acidic decomposition products. On such sites polyphenol production will be low. These conditions favour an increased proportion of bacteria, relative to fungi, in the decomposer community, and a greater and more diverse soil mesofauna (Pritchett, 1979). Humification of plant residues is more complete and mesofaunal activity results in considerable mixing of organic material with the mineral soil, so that there is no distinct mineral/organic boundary. These processes give rise to mull humus formation (Figure 2).

Where the available N capital of a site is low, N uptake, net primary production and litter inputs will also be low. The concentration and quantity of N in foliage and litter will be correspondingly low, although low N concentrations in the litter may not reflect greater withdrawal. Polyphenol production will tend to be high because of either a stress-induced physiological change within a species, or a change of species in response to poor site conditions (Gosz, 1981). Because of poor litter quality, rates of decomposition and N release are low and the limited supply of available N results in intense heterotrophic competition. Under these conditions nitrifying populations and rates of nitrification will be extremely low.

Low N availability is common on acid, base-poor soils where available calcium levels will be low. A high proportion of polyphenols will therefore remain active while the soil's capacity to neutralize acidic decomposition products will be low. The acid conditions and recalcitrant nature of the litter favour the dominance of fungi in the decomposer community, and mesofaunal activity (particularly earthworms) is low. Litter accumulates into distinct L, F and H horizons and there is virtually no mixing of organic material with the mineral soil, resulting in mor humus formation (Figure 2).

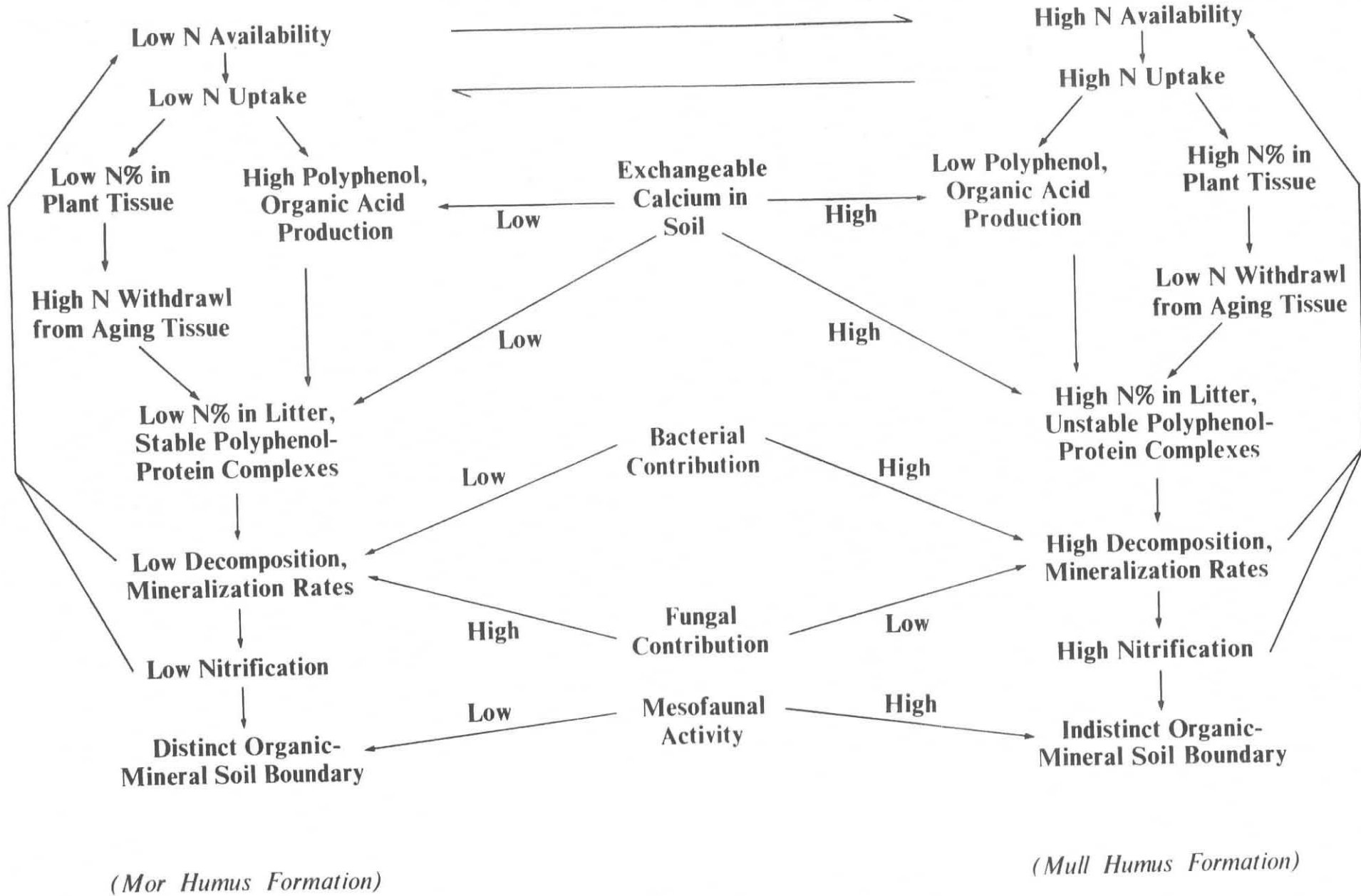


Fig. 2 Processes governing nitrogen cycling and humus development in forest ecosystems (after Gosz, 1981)

Between these extremes a range of intermediates can occur, while a shift in either direction may result either from species change or from changes in nutrient availability. Such changes may take place naturally, as during a succession, or may be a consequence of management operations, e.g. fertilizing or liming.

The application of N fertilizer is followed by a rapid distribution of the N applied to the tree crop, competing vegetation, forest floor and mineral soil. Losses of N fertilizer are low at normal commercial rates of application (Miller, 1981). Where trees are N stressed the application of N fertilizer causes a growth response which normally lasts 5-10 years, although this may be only 3-4 years on particularly deficient sites (Fagerstrom & Lohm, 1977; McIntosh, 1983). Growth then falls to its pre-fertilizer rate, i.e. there is no long-term effect on N availability, N circulation, or site productivity. Long-term effects will only occur where the quantity of N applied is large in relation to the original N capital of the site. Except on the most deficient sites commercial rates of N fertilizer application are too low to result in permanent change (Miller, 1981).

## VI. Decomposition, nitrogen mineralization and nitrogen immobilization

### 1. Introduction and definitions

The release of N from litter is a basic process in the cycling of N within an ecosystem. Virtually all the N taken up by plants is inorganic and the continual replenishment of the pool requires that inorganic N is released from litter during decomposition.

The decomposition process may be defined as the biologically-mediated breakdown of an organic substrate. In this process, carbon and other elements released from the substrate are used to support microbial respiration and the synthesis of microbial tissue. Decomposition results in a continuous decline in substrate mass. N mineralization is the biologically-mediated release of organically bound N from a substrate and its conversion to the inorganic forms ammonium and nitrate. The release of organically-bound amino-N is termed proteolysis while its subsequent reduction to ammonium is ammonification, although this latter term may be used to include both these steps (Mengel & Kirkby, 1982). Under certain conditions ammonium may be further reduced to nitrate. N immobilization is the conversion of inorganic N to organic forms and is normally applied to the uptake of inorganic N for the synthesis of microbial tissue.

Although the N content of a substrate will begin to decline once decomposition has commenced this may not be associated with a net release of N to the soil inorganic N pool (i.e. net mineralization). The microbial biomass is highly dynamic and there is a continuous transfer of mineralized N into microbial tissue and a simultaneous release of immobilized N, upon cell death, into the inorganic N pool. A net change in this pool, net mineralization or net immobilization, depends on the balance between the simultaneous processes of gross mineralization and gross immobilization. Thus a low rate of net mineralization may reflect either a low rate of microbial activity or a high rate of activity where the processes act in opposite directions (Jansson & Persson, 1982).

Net mineralization will usually only occur when the N released from a decomposing substrate exceeds that required by the microflora. This occurs when the substrate C : N ratio approaches or falls below that of the microbial biomass; more N is then released per unit of substrate carbon than can be used in the synthesis of microbial tissue, and the availability of carbon has become the major growth determinant. When substrate C : N ratios exceed those of the microflora, net immobilization occurs.

### 2. Environmental influences on decomposition and mineralization

#### (a) Decomposition and ammonification

Since the processes of decomposition and ammonification are mediated by the same organisms the influence of environment is essentially the same for both. Thus in the following discussion comments concerning the influence of environment on ammonification are equally applicable to decomposition. However, under certain conditions, such as a rapidly expanding microflora, decomposition and gross ammonification will occur without net ammonification because of the immobilization of N in microbial tissue.

A very wide range of heterotrophic microbes is involved in ammonification and they possess considerable biochemical diversity (Heal, 1979). Because of this diversity ammonification is seldom eliminated although the rate may be influenced by environment.

The general relationship between environmental factors and ammonification has been known for some time (Waksman & Gerretsen, 1931; Harmsen & Schreven, 1955; Witkamp, 1966). Since ammonifying populations contain aerobes and anaerobes, ammonification proceeds over a wide range of oxygen and moisture conditions. Under anaerobic conditions more ammonium may accumulate



since microbial growth is depressed, which reduces immobilization without necessarily reducing mineralization (Ponnamperuma, 1972). This fact has been exploited by anaerobic incubation techniques, used to assess potentially mineralizable N (Waring & Bremner, 1964). Excessively dry conditions, approaching wilting point, inhibit ammonification (Alexander, 1977; Hopmans *et al.*, 1980), although certain systems appear to be able to function under unusually dry conditions (Nagy & Macauley, 1982). Clarholm *et al.* (1981) found a positive relation between inorganic N concentration and moisture content, over the range 20–100% of the water holding capacity of a pine forest podsol. For a wide range of soils optimum moisture content for ammonification is between 50 and 75% of the water holding capacity (Alexander, 1977).

Ammonification is enhanced by cycles of drying and wetting (Birch, 1964), total inorganic N release generally increasing with the duration of the dry phase (McColl, 1973). This response is in part due to physical disruption of the organic material but is primarily a result of a partial sterilization effect on the biomass; killed cells undergo lysis or rapid breakdown by the remaining microbes and this results in a carbon dioxide and nutrient flux. These fluxes have been shown to be proportional to the size of the initial biomass, and the effect has been used to assess the size and nutrient content of the soil biomass pool (e.g. Brookes *et al.*, 1982). Similar fluxes occur after any soil disturbance which results in the death of some fraction of the biomass, e.g. freezing and thawing (Birch, 1964; Witkamp, 1969) or grinding and cultivation (Powlson, 1980).

Microbial respiration increases with temperature and is directly related to the mineralization of physiologically active plant nutrients (Witkamp, 1966; Wollum & Davey, 1975), maximum rates of ammonification occurring between 40 and 60°C. Many workers have demonstrated the importance of temperature (Kai *et al.*, 1969; Bulgen, 1982), which can be the major limiting factor under cold conditions (Moore, 1981; Cleve *et al.*, 1981). Temperature and moisture show considerable interaction in their influence on microbial respiration (Bunnell *et al.*, 1977). The interaction is maximal at high temperatures and moisture contents with the response to temperature declining at low moisture content and vice versa. Meentemeyer (1978) demonstrated the importance of this interaction, showing that on a macro-climatic scale, litter decomposition is highly correlated with actual evapotranspiration, which is effectively a combined index of energy (temperature) and moisture.

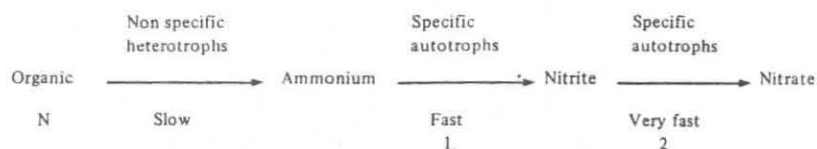
Ammonification is generally favoured by neutral environments and depressed by acid conditions, being higher in soil with mull humus than those with moder, mor or peat (Laune *et al.*, 1981; Lodhi, 1982). Many workers have reported an increase in ammonification after the application of lime to acid soils, although it may be shortlived under forest conditions (Nommik, 1978; Keeney, 1980; Carey *et al.*, 1981; Robertson, 1982).

The presence of inorganic and organic metabolites influences microbial growth and ammonification, which may be enhanced in the rhizosphere in the presence of root exudates (Rambelli, 1973). Clarholm & Rosswall (1980) found that spring and autumn peaks in the number of soil fungi and bacteria were associated with rainfall, even when moisture was not limiting. They concluded that this was because of inorganic and organic material present in rain or leached from foliage.

## (b) Nitrification

Several extensive reviews have been published on nitrification including the biochemical aspects (Focht & Verstraete, 1977), ecological aspects (Verstraete, 1981), microbial aspects (Alexander, 1977), and nitrification in agricultural soils (Schmidt, 1982) and in forest ecosystems (Robertson, 1982).

The initial product of mineralization of organic N is ammonium. Depending on the environmental conditions this may be the end product, or it may be oxidized by microbes to produce nitrate, e.g.



In contrast to ammonification the oxidation of ammonium and subsequent further oxidation to nitrate is mediated largely by a restricted group of aerobic autotrophic bacteria which derive energy from the conversion (Robertson, 1982). Consequently, rates of nitrification are markedly influenced by environment.

Step 1 is known to be carried out by the genera *Nitrosomonas*, *Nitrosococcus*, *Nitrospira* and *Nitrosolobus* (Focht & Verstraete, 1977) while step 2 is carried out by the genus *Nitrobacter* (Alexander, 1977). Only *Nitrosomonas* and *Nitrobacter* occur commonly in soils. Since nitrite does not occur as more than traces in terrestrial ecosystems there is strong evidence that ammonium and nitrite oxidizers normally occur together. Certain methane oxidizing bacteria have been associated with ammonium oxidation and these organisms can occur under more acid conditions than the groups mentioned above, but their significance is uncertain (Verstraete, 1981; Schmidt, 1982). A wide range

of heterotrophic bacteria and actinomycetes can oxidize ammonium to nitrite but only in trace amounts, and since at least two fungal genera can oxidize nitrite, an entirely heterotrophic pathway is possible in a mixed microbial population (Alexander, 1977).

Rates of nitrification vary markedly between ecosystems but a low rate of nitrification is central to N conservation (Likens *et al.*, 1969; Vitousek *et al.*, 1979, 1982). Nitrate is more readily lost from ecosystems than ammonium. Also hydrogen ion production during nitrification can lead to increased cation loss; it can increase the concentration of base cations in solution as a result of cation exchange.

Factors influencing nitrification in both disturbed and undisturbed ecosystems have received considerable recent attention, because of the potential for N loss that they create (Jones & Richards, 1977; Lohdi & Killingbeck, 1980; Khanna, 1981; Matson & Vitousek, 1981; Adams & Attiwill, 1982). Six major environmental factors influence autotrophic nitrification in well-aerated soils (autotrophic nitrifiers are obligate aerobes and cannot nitrify under anaerobic conditions). The influence may be positive (+) or negative (-): temperature (+); moisture (+), pH (+), amount of substrate (+), nutrient supply (+), and allelochemicals (-).

Amount of substrate is especially important in forests where rapid immobilization is caused by litter of high C:N ratio coupled with readily oxidizable carbon and a strongly competitive heterotrophic microflora. Competition for ammonium may be increased by mycorrhizae, which can compete very effectively for low concentrations of nutrients and may suppress other microflora (Gadgil & Gadgil, 1978). Under such conditions populations of nitrifiers, which are poor competitors for ammonium (Jones & Richards, 1977), are low. This inability to compete for low concentrations of ammonium is probably the dominant control on nitrification in most ecosystems (Adams & Attiwill, 1982; Vitousek *et al.*, 1982).

Soil pH has long been considered an important factor restricting nitrification (Alexander, 1977; Keeney, 1980), which is progressively inhibited below pH 6. However, nitrate is commonly detected in acid soils down to pH 4.5 (Robertson, 1982). This could result from methylotrophic or heterotrophic nitrification but there is little direct evidence for this theory (Verstraete, 1981). It is likely that bulk pH measurements are inadequate predictors of nitrification, which may take place at microsites of high pH in an otherwise acid matrix. Recent evidence also suggests that autotrophic nitrifiers exhibit greater ecological and phenotypic diversity than was previously supposed (Verstraete, 1981; Robertson, 1982). It is probable that nitrifying populations can evolve *in situ*, to become adapted to local soil conditions, so that the inability of a population from a neutral environment to nitrify under acid conditions may not reflect the ability of a population which has developed in an acid soil (Robertson, 1982).

In agricultural soil, nitrification is commonly influenced by nutrient availability, phosphorus being especially important (Schmidt, 1982). It is likely that mycorrhizae, with their pronounced affinity for phosphorus, may exert a further control on nitrification. Allelopathic controls have been frequently suggested (Rice & Pancholy, 1974; Lodhi & Killingbeck, 1980 but doubt has been cast on many of the techniques upon which such suggestions have been based (Robertson, 1982).

The restricted nitrification in many forest ecosystems is reflected in the low rates of nitrate export that have been found by many workers (Feller, 1977; Sollins *et al.*, 1980; Sollins & McCorkison, 1981). Where nitrification occurs readily, N losses can be high (Melillo *et al.*, 1981).

### 3. The influence of litter quality on decomposition and mineralization

N release from litter is a basic process in the cycling of N within an ecosystem. Litter quality, soil organisms and environment regulate decomposition and therefore nutrient release (Heal 1979; Berg & Staaf, 1980, 1981; Staaf & Berg, 1981; Heal *et al.*, 1982; Berg & Ekbohm, 1983).

The influence of specific environmental factors has already been discussed. Litter quality refers to those physico-chemical characteristics which influence decomposition. These include the nature of the carbon source, nutrient sources, modifying compounds and physical properties. Litter quality varies between and within species, depending also on the site conditions (Berg & Ekbohm, 1983) and age (McGill *et al.*, 1981). It also varies between components of the same plant (Heal, 1979). Physical properties of the litter which influence decomposition are surface toughness, particle size (surface area) and, in particular, moisture uptake. The last is influenced by the amount of physical contact with the soil and therefore particle size (Kaarik, 1974). Conifer needles have a hydrophobic surface and small surface area, and as a result they may be slow to take up moisture, but are effective at retaining it. They retain their surface integrity for longer than broadleaved leaf litter, which is readily wetted but does not retain moisture to the same extent (Heal, 1979).

A wide range of organic compounds can act as carbon and energy sources for microbes. The ease with which a given substrate can be decomposed depends heavily on the properties of its organic constituents (Minderman, 1968). Water-soluble and acetone-soluble components such as sugars, amino acids, steryl esters and triglycerides decompose first, disappearing almost completely within the first year. These are followed by celluloses and hemicelluloses and then by lignin (Reber & Schara, 1971; Berg, 1978; Berg & Staaf, 1981; Berg *et al.*, 1982b, 1982c).

Polyphenols and phenols may take even longer to decompose (Minderman, 1968; Reber & Schara, 1971) although polyphenol content may decrease during the first year, with an initially rapid



fall (Hayes, 1965). The recalcitrance of polyphenols may result from their apparent inhibition of fungal growth (Berg *et al.*, 1980, 1982c).

Although many substances are involved the rate of decomposition (assessed as CO<sub>2</sub> flux or weight loss) of carbonaceous material is strongly influenced by the proportion of lignin (Fogel & Cromack, 1977; Meentemeyer, 1978; Parkinson, 1979; Aber & Melillo, 1980; Berg *et al.*, 1982c), which decomposes 5 to 10 times more slowly than other more soluble compounds. Bunnell *et al.*, (1977) accurately modelled weight loss from decomposing litter using a double exponential model to express both rapid and slow rates of decomposition and a similar approach has been used by other workers (McGill *et al.*, 1981).

The reasons for the recalcitrance of lignin are discussed in detail in a review by Zeikus (1981). Lignin is one of the last substances to start to decompose, so its concentration increases relative to those substances which exhibit rapid weight loss. In needle litters no lignin loss may occur until 40-45% of initial needle weight has been lost, i.e. until lignin concentration has reached around 30% (Fogel & Cromack, 1977). Even after lignin has begun to decompose it does so more slowly than other organic fractions, so that its concentration still continues to rise (Berg & Staaf, 1980, 1981; Berg *et al.*, 1982c; Melillo *et al.*, 1982). Lignin can also reduce the decomposition rates of more labile compounds which it may enclose structurally, rendering them resistant to microbial attack (Nilsson, 1973; Zeikus, 1981). Because of its recalcitrance, lignin decomposition is rate-determining for the weight loss of most litter (Parkinson, 1979; Berg *et al.*, 1982c; Melillo *et al.*, 1982). High proportions of lignin or high lignin : N ratios are associated with low decomposition rates (Aber & Melillo, 1980). Highly lignified material such as bark and wood decomposes very slowly (Foster & Lang, 1982; Heal *et al.*, 1982), so that most soil organic matter reflects their unique isotopic ratios (Waring, 1980). In vascular plants lignin may account for 25% of dry weight and ligneous litterfall may account for 80% of primary production in some forests (Zeikus, 1981).

For a long time it has been known that N contents are correlated with rates of decomposition, weight loss being more rapid for litter with a high N content (Melin, 1930; Witkamp, 1966; Heal, 1979; Berg & Staaf, 1981). However, other workers have found the lignin level to be more rate-determining (Fogel & Cromack, 1977; Melillo *et al.*, 1982). Hermann *et al.* (1977) found that weight loss was more highly correlated with the lignin : carbohydrate ratio than it was with the C : N ratio. Initial weight loss (up to 30% of initial weight), largely the decomposition of soluble compounds, cellulose and hemicellulose, is strongly correlated with N (and other nutrient) concentrations. Once lignin starts to decompose the effect of N in accelerating weight loss appears to be masked by the slow decomposition of lignin. Recent work (Berg *et al.*, 1982b) indicates that lignin decomposition is actually depressed in litter that had a high initial N concentration. There appears to be an inhibitory effect of ammonium on the ligninolytic enzyme systems of microbes (Keyser *et al.*, 1978); the rate of decomposition is shown to decrease after ammonium application (Bengtsson, 1936). Ligneous material can also fix ammonium, leading to the formation of heterocyclic ring compounds which are highly resistant to microbial degradation. Such fixation is indicated by Berg & Staaf (1981), who found that the increase in litter N content during decomposition was linearly correlated with an increase in lignin-bound N. Thus while initial weight loss may be well correlated with N content (Aber & Melillo, 1980), except where external N sources are abundant (Melillo *et al.*, 1982), the situation becomes reversed once the decomposition of lignin has started.

N release from decomposing litter is essentially regulated by the same factors as decomposition, but is modified by immobilization. The pattern of N release from litter follows three phases, although not all need occur under a given set of conditions (Berg & Staaf, 1981). Before and during litterfall, epidermis integrity may be reduced by the leaf surface microflora; very early weight loss and N release then result from the physical leaching of soluble compounds (Nykqvist, 1963). The quantity of leachable N appears to be 2-4% of the total N, irrespective of the amount (Berg & Staaf, 1981). Since this leachable fraction has a very rapid turnover (Berg, 1978), it is likely that some of it is decomposed within the litter, particularly in the case of conifer needles (Nykqvist, 1963). Early release of N as a consequence of leaching is normally associated with high N concentration in the litter, but Berg & Staaf (1980) report leaching loss at a litter N concentration of 0.58%.

An increase in the N concentration of decomposing litter is a well-known phenomenon (Bocock, 1963; Gosz *et al.*, 1973) which can occur whether there is a release of N or not (Berg & Staaf, 1981). It results from a loss of carbon through respiration while N is retained by microbes. An absolute increase in the amount of N may also occur. Such accumulation (immobilization) starts early during decomposition and tends to continue up to approximately 35% weight loss (Howard & Howard, 1974; Berg & Staaf, 1981). For Scots pine needles the period of N accumulation is associated with the invasion of fungal hyphae (Berg & Staaf, 1979). Postulated sources for this N are: N fixation; absorption of atmospheric ammonia; throughfall; dust; insect frass; green litter; and fungal translocation/immobilization (Howard & Howard, 1974; Melillo *et al.*, 1982). While the N concentration and absolute N content of the substrate plus microbial biomass may increase, the quantity of N in the substrate itself will decrease with time, when it is immobilized as microbial N or secondary organic products (Swift *et al.*, 1979; Heal *et al.*, 1982).

The initial N content of litter definitely influences whether or not immobilization takes place. However, a critical N value above which accumulation does not occur (Mulder *et al.*, 1969) may not

be generally applicable to a forest system. The use of C : N ratios to predict patterns of immobilization/mineralization in agricultural soils appears to work well (Jansson, 1958; Paul & Juma, 1981). Mineralization occurs below C : N 25 and immobilization above C : N 35, the net change being relatively unaffected by intermediate values (Heal *et al.*, 1982). These patterns result from microbial demand for N during growth while carbon is being used. The substrate provides N when the concentration is high, and N in excess of microbial requirements is released by deamination (more generally termed ammonification). Immobilization occurs when the organic N of the substrate is low (Alexander, 1977). The N concentration of material with C : N ratios above 35 increases until a critical value (in the range C : N 25-35) is reached when N release occurs. This classical model does not describe N behaviour in forests adequately (Berg & Staaf, 1981; Heal *et al.*, 1982), where accumulation occurs at initial N concentrations ranging from 0.3 to 1.4%, the latter value appearing to be an upper limit (Berg & Staaf, 1981).

Accumulation is related to microbial processes and has been shown to be linearly correlated with weight loss (Berg & Staaf, 1981), i.e. to microbial activity. Accumulation also increases at high lignin concentrations. Melillo *et al.*, (1982) found that more N was immobilized, per unit of carbon respired, the higher the initial lignin concentration. The influence of environment seems especially important; Anderson (1973) found that N accumulation in beech leaves incubated on soil was twice that of those incubated in air; Dowding (1974) found that barley straw accumulated N up to 170 and 230% of its original N content at two tundra sites, while on a third site there was no accumulation; Berg & Ekbohm (1983) found that the critical C : N ratio, above which there was net immobilization and below which there was net mineralization differed between a clear-felled (C : N 63) and a forested (C : N 109) site.

Accumulation is followed by N release, although N concentrations can continue to rise after a net release has occurred. The N concentration at which release occurs varies markedly between forest types but can be as low as 0.7-0.8% (Berg & Staaf, 1981). Once N release has started it is linearly correlated with weight loss. As in the case of accumulation, the critical concentration for N release depends on site. It increases with the rate of first year weight loss (Berg & Staaf, 1981); this is probably a conservation mechanism to prevent N loss on sites where decomposition is rapid.

From what has been said, it is clear that a high litter input, low in N but high in lignin (containing a large proportion of wood), will give low rates of decomposition and N release. Under such conditions considerable litter accumulation may occur (Witkamp & Ausmus, 1976). The contribution of large woody components is often underestimated (Richards, 1981; Graham & Cromack, 1982) but their contribution in terms of biomass and N returned to the forest floor can be large, increasing as the stand matures (Gessel & Turner, 1976). Such woody materials may be exceptionally low in N and this, combined with organic recalcitrance, results in very low rates of decomposition and prolonged N immobilization (Vitousek, 1982). Fungi dominate in the decomposition of woody substrates, and all substrate N may have to be converted to mycelium before release can occur (Kaarik, 1974; Richards, 1981; Heal *et al.*, 1982), a process which may take 20 years, during which time this portion of the litter can act as a sink for mineralized N (Graham & Cromack, 1982).

There is comparatively little information on the decomposition of fine roots, although it is assumed to be controlled by the same factors as influence the decomposition of above-ground litter (Gosz, 1981). N concentrations in fine roots and mycorrhizae have been reviewed by Fogel (1980) and Kimmins & Hawkes (1978). They range from 0.33 to 2.03%, so that one might expect rapid release or slow release of N depending on where a sample lay in this range. It is not known whether fine roots undergo physiological changes associated with abscission analogous to the changes undergone by foliage (Fogel, 1983); if they do this would obviously influence their rate of decomposition.

McClagherty *et al.* (1984) showed that fine roots of less than 0.5mm diameter decomposed more rapidly than larger roots. Initial mass loss (10-20%) was rapid but rates then slowed so that only 20-60% of root mass was lost after four years. Root decay could be represented by a composite exponential model, including a labile and a recalcitrant fraction. Berg *et al.* (1982a) found first year loss of fine root litter to be 32% while Popovic (1980) associated fine roots with slow decomposition and N immobilization. Carbon released during the decomposition of fine roots may be 2.0-2.8 times that from above-ground litter, representing 42% of the annual carbon turnover in some forest ecosystems (Edwards & Harris, 1977). N release during the decomposition of fine roots may be 1.4-2.0 times that from above-ground sources (Henderson & Harris, 1975; Wells & Jorgensen, 1975). Fogel (1983) found that mycorrhizae and fine roots accounted for 43% of N release in a Douglas fir stand.

#### 4. Nitrogen mineralization, interactions between the microflora and soil fauna

The importance of the microflora in the cycling of nutrients in soil systems has been comprehensively reviewed by Coleman *et al.* (1983). Measured rates of annual N mineralization in forest ecosystems range from 30 to 50 kg/ha for conifers and from 100 to 300 kg/ha for deciduous broadleaves (Gosz, 1981). Sites where temperature or moisture are limiting may have lower rates e.g. 3.9-1.6 kg/ha (Popovic, 1980) or 11.5 kg/ha (Rapp *et al.*, 1979). Such values are based on incubation techniques

which only measure net mineralization, i.e. N released in excess of microbial requirement, and do not account for turnover of N within the microbial biomass (Paul & Juma, 1981; Heal *et al.*, 1982).

N incorporated into the microbial biomass is temporarily immobilized, immobilization normally being associated with an actively increasing biomass (Clarholm *et al.*, 1981). Fungal tissue may be 2.2–19.6% N and can account for 160–1430 kg/ha of soil N (Baath & Soderstrom, 1979). Frequently, sequential measurements of the microbial standing crop show little change in pool size, but tracer techniques (Paul & Juma, 1981) and observation of respiration rates (Clarholm *et al.*, 1981) indicate rapid turnover (Anderson *et al.*, 1981). The reason for this rapid turnover is grazing by the soil fauna. The actively proliferating microflora is maintained as a relatively small standing crop with a very rapid turnover (Parkinson, 1979; Anderson & Ineson, 1982). The soil fauna excrete N-rich substances and increase the homogeneity of decomposer distribution, thus maximising substrate utilization and increasing N availability (Anderson *et al.*, 1981).

N turnover between the substrate and the microbial biomass plus soil fauna considerably exceeds net mineralization. For example estimates of gross annual mineralization may be as high as 591 kg/ha (Heal *et al.*, 1982), far in excess of plant requirements (Cole & Rapp, 1981). This N is potentially available to plants, in competition with soil saprophytes.

Fungi dominate in acid forest situations. Their nutritional requirements are extremely diverse (Richards, 1981; Baath & Soderstrom, 1982). Many are able to decompose materials with extremely low N concentrations, perhaps by transferring N from N-rich substrates (Berg & Staff, 1981). N immobilized in fungal tissue can be released by lysis and faunal grazing, even when C:N ratios are high (>35). Many fungi are able to utilize soluble organic N after the initial breakdown of large molecules, deamination then occurring within the mycelium. Thus N turnover can be accomplished without the need for an inorganic pool. Mycorrhizae can also utilize organic N in compounds of low molecular weight (Bowen, 1981; Bowen & Smith, 1981; Alexander, 1982) enabling plants to compete with saprophagous fungi for a soluble organic N pool. Recent work (Cleve & White, 1980) indicates that this pool may be appreciable, 40 kg/ha, representing nearly 10% of total system N. Their work has indicated that much of this organic N does not pass through the inorganic pool, suggesting that there is uptake of organic N by saprophytic and mycorrhizal fungi (Heal *et al.*, 1982).

It has been suggested that the rhizosphere of certain tree species can mineralize or somehow make available a fraction of soil organic N that is resistant to microbial breakdown under other vegetation types. The magnitude of this rhizosphere effect varies with species, but it seems most developed for pioneers such as larch and pine, and less developed for spruce (Stone & Fisher, 1969; Fisher & Eastburn, 1974; Jones & Richards, 1977 and 1978; Gosz, 1981; Skinner & Attiwill, 1981; Yeates *et al.*, 1981). Since mycorrhizae can exploit very little humus-bound N (Lundberg, 1970) it seems likely that rhizosphere microbes are primarily responsible for this increased mineralization.

## 5. The influence of management operations

Various silvicultural operations conducted in managed forest will influence the processes of decomposition and mineralization. These will be briefly considered in the sequence in which they are likely to occur during the life of a crop.

Starting with an unforested site, establishment operations such as ploughing and drainage are likely to cause a pulse of increased mineralization of native organic N. This will occur because of a partial sterilization effect, exposure of previously unavailable substrate, an input of killed vegetation, and improved physical conditions for microbial activity (Heal, 1979; Powlson, 1980). On some sites this initial flush of mineralized N may remove the need for early N fertilizing. However, because of small tree size and limited site occupancy by the crop, only a small proportion of this mobilized N will be taken up by the trees. Depending on site conditions the remainder may be held by the soil, lost, or retained by the ground flora. Sites low in organic matter and total N may be particularly sensitive to cultivation in terms of future productivity (Bevage, 1980).

Fertilizer applications with elements other than N have been shown to stimulate N mineralization on some sites (Carey *et al.*, 1981). N fertilizer will also stimulate the mineralization of native N (Jansson & Persson, 1982) but the amounts will be small in relation to the N applied.

Weed control is likely to enhance N mineralization through the input of N-rich substrate. The removal of weeds may also increase the amplitude of physical cycles at the soil surface and reduce competition for water and nutrients, both of which effects will stimulate mineralization.

After canopy closure increased mineralization might be expected to follow thinnings as a result of the input of green litter and short-term increases in the variation of temperature and moisture (Heal, 1979). A similar, but larger, effect might be expected from clear felling, as has been previously discussed.

## VII. Conclusions

The N cycle in forests is characterized by a large N capital but low concentrations of available N, with cycling operating to maximize the use of the available pool and maintain it, while minimizing losses from the system. Differences in cycling between forest types largely reflect differences in N capital which have resulted from the differential accumulation of atmospheric N. Accumulation is a function of ecosystem age and environmental factors which promote or inhibit N input from the atmosphere. Where two sites have widely different N capitals they will normally support different species, e.g. conifers as opposed to broadleaves. Where differences are less the same species may occupy both sites although the form and rate of cycling may differ.

Where N capital is high, both transfers between ecosystem compartments and rates of mineralization tend to be correspondingly high. The result is a high concentration of available N which permits some nitrification to occur. Loss is controlled by high uptake rates, and N concentrations in the tree biomass and litter are large. Conversely, a low N capital means that absolute N transfers between compartments are small, although in relative terms they may not differ from sites of high N capital. Some research does indicate a greater dependence on within-tree cycling and a lesser dependence on between-compartment cycling where N capitals are low, but other workers refute this. It is because they are more efficient than deciduous broadleaved species in their use of N that conifers tend to dominate on N-poor sites.

A considerable amount of information now exists concerning the N capital and productivity of different ecosystem compartments and N transfers between compartments. A notable exception is the fine root system which has only recently attracted the research attention that it deserves. The influence of environmental factors on the basic processes of decomposition and mineralization is well established, and further research in this area is unlikely to yield anything new. Similarly, the gross effects of litter quality are also well known and further advances are only likely at the biochemical level. However, a detailed consideration of the interaction between these factors and the dynamics of different populations within the microbial community has rarely been undertaken.

Basic information on the processes of nitrification, and more particularly of denitrification is lacking for many forest ecosystems. Many assumptions are based on findings for agricultural soils which may not be applicable to forests.

Fungi dominate the decomposition process in many forest soils. Their ability to degrade recalcitrant substrates, combined with the activity of saprophytic grazers, can result in N release from litter of high C:N ratio. Such interactions, and the ability of trees and their mycorrhizae to compete for gross mineralization products, or to exploit soluble organic N, need to be fully investigated.

Sufficient background information from ecosystem and process-orientated research now exists for useful generalizations to be made concerning the influence of management practices on the forest N cycle. However, site specific predictions will require the collection of site specific data if more precise statements are to be made. Similarly, manipulations of the N cycle to increase forest production without the use of N fertilizer, such as the use of N-fixing associations, is possible in theory, but further research or the development of new technologies may be required if measures of this kind are to work in practice.

There is still some confusion over the effect of fertilizers on N cycling and site productivity. Permanent increases in site productivity, as distinct from short term increases in crop production, will only occur where N additions are large relative to the existing N capital of the site. In this respect N fertilizer applications at normal management rates may be thought of as being applied to the tree crop and not the site (Miller, 1981). Little research has been directed to increasing site productivity by improving the mineralization of bound N and the rate of N cycling. At its simplest this has been attempted by lime application to acid sites, while more involved methods might include the use of species mixtures (O'Carroll, 1978).

Further process-orientated research, particularly of forest floor interactions, will increase our understanding of N cycling in forests. However, much useful information already exists which, if it were more generally available, could aid decision making by forest managers and help them to reduce unwanted effects.

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